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PULLMAN, WASHINGTON

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Studies on the Relation of Certain Species of Fusarium to the Tomato Blight of the Pacific Northwest

By

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BULLETIN NO. 115
October, 1914

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STUDIES ON THE RELATION OF CERTAIN SPECIES OF FUSARIUM TO THE TOMATO BLIGHT OF THE PACIFIC NORTHWEST

By H. B. HUMPHREY,* Ph.D., PLANT PATHOLOGIST

INTRODUCTION

Certain of the *Solanaceae* are peculiarly susceptible to diseases of the roots or other subterranean organs; and foremost among these may be placed the tomato and potato. Often, as for example, in the dry end rot of the potato and the so-called Southern tomato blight described by Smith† as occurring in California, two or more diseases may be induced by one and the same organism. Particularly is this true when the causative organism is a species of Fusarium.

The tomato blight of the Pacific Northwest referred to throughout this Bulletin as the Yellow Blight of the tomato, is due primarily to root-destroying fungi, and should not be confused with the disease known as Sleepy Sickness, so prevalent throughout certain of the Central and Southern States. Geographically, it appears to be confined to the Pacific Northwest; and even here is most epidemic and virulent in those localities where high July and August temperatures prevail. For example: Tomatoes grown from the same variety and lot of seed, but transplanted part in the soil of the Snake River bottom land and the remainder near Pullman, Washington, may blight severely in the former situation and not at all or but little at the higher, and noticeably cooler elevation. A like difference in severity obtains when we compare notes relative to prevalence of the disease in the Yakima Valley and the country about Pullman.

Tomato-growing in the valleys of the Snake, Columbia, and Yakima Rivers constitutes an important source of income, notwithstanding the fact that in years of severe blight the loss may average in some localities as much as 30 to 50% of the total crop. The recurrence of severe blight epidemics from year to year led the Washington State Experiment Station in 1896 to undertake an investigation of the disease, its cause or causes, and possible means of control.

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*Resigned March, 1913.

†Smith, R. E. 1906. Tomato Diseases in California. Bull. 175 Cal. Agr. Exp. Sta.

HISTORY

From 1896 to 1902 the project was in charge of C. V. Piper, then Botanist of the Washington State Experiment Station. Piper's notes indicate his belief at that time in a bacterial causation of the disease, and he isolated several pure cultures of bacteria from diseased plants. In one series of inoculation experiments with one of these organisms several of the treated plants acquired all the symptoms of the blight, but in subsequent attempts to produce the disease with the same specific organism the results were purely negative. The data were never published.

Piper also tested a large number of tomato varieties in the Yakima Valley with a view to discovering a blight resistant strain. These showed a wide variation in susceptibility to the disease, but all varieties tested suffered a considerable percentage of blighted plants.

Following Piper, his successor, R. Kent Beattie, assisted by N. R. Hunt, continued along lines of investigation of a somewhat more comprehensive character. They made continued and frequent unsuccessful attempts to recover from diseased foliage and shoots the suspected parasite, apparently adhering to the theory of a bacterial origin of the disease. Carefully conducted field studies were made during the summer of 1907 with a view to ascertaining the nature and extent of the influence of environmental conditions. During the same season observations were also made with reference to the relative resistance capacities of different standard varieties*.

In 1909 the project was assigned to the writer. Although there still remain many points of interest needing further study, it may be assumed that the investigation has advanced sufficiently to warrant the publication of such data as have been recorded during the past five years.

DISTRIBUTION OF THE YELLOW BLIGHT

As stated on another page, the yellow blight of the tomato is most general and destructive in those parts of the Pacific Northwest subject to prolonged periods of high summer temperature. It seems also to be a fact that light, quickly heated soils, other factors aside, afford a more favorable environment for the incubation of the causative organisms than is true of the heavier, more compact soils which are less readily aerated and more slowly heated.

The disease known as "Summer Blight," common throughout the larger agricultural valleys of California and described by Smith*, '06, is probably not identical with the disease described in this bulletin,

*The results of these studies will be incorporated in a subsequent bulletin dealing with the subject of Breeding and Selection for Disease Resistance in Tomatoes.

*Smith, R. E. Tomato Diseases in California. Bulletin 175, Jan. 1906.

although the seat of fungus growth and activity is confined to the same part of the host plant, namely, the root system. To the writer's knowledge, the occurrence of yellow blight has not been reported from any state east or south of Oregon, Washington, and Idaho.

SYMPTOMATOLOGY

During the incipient stages of the disease, the host, while producing its first flowers, or in many instances, after its fruit is a third or half-grown, begins to show first symptoms; *i. e.*, a slight torsion of the entire leaf accompanied by a purpling of the leaf veins. With the general torsion of the leaves, one may also observe a twisting and rolling inward followed by drooping (not wilt) of the leaflets and leaves. The lower leaves of field-grown plants are not necessarily the first to become yellow. They not infrequently remain green for several days after leaves of subsequent growth have begun to fade and die. Even in the latest stages of the disease the foliage does not wilt, but seems to become brittle, at first taking on a glaucous sheen which from a distance gives the afflicted plant a greyish appearance. Immature tomatoes, one-half inch or less in diameter, become yellow and ultimately take on a depth of color indicative of ripeness. The pulp of these tomatoes is quite agreeable to the taste, though it lacks the aroma and palatable flavor of a fully matured and properly ripened tomato. The seeds of these small fruits fail to develop. With the onset of the blight there is a marked cessation of growth, and all affected plants assume an erect habit, excepting those cases in which the invasion of the root system occurs late in the season after the host has borne heavily and has become prone from heavy fruitage.

Plants suffering from the yellow blight, but grown under conditions which obtain in the average greenhouse, do not present in anything like so striking a degree the symptoms manifested by plants of the same variety when grown in the field. Our studies have progressed sufficiently to justify the opinion that such factors as soil temperature and moisture, wind movement, air temperature, and light intensity are the controlling factors in this disease. In our greenhouse experiments we have been able to produce yellow blight, but never have these experiments yielded blighting plants which would present the same symtomatic complex as those grown under out-door conditions. And there is no reason why they should; the soil temperature in the greenhouses where our experiments were conducted was rarely if ever as high as the optimum temperature (86° F.) of the causative organisms. Hence, fungous growth within the roots was more or less inhibited. It must also be patent enough that growth conditions affecting the host when grown in a greenhouse are so nearly ideal as to afford it a far better fighting chance against invading fungi.

Infected plants maintained in the greenhouse manifest the first signs of blight in the twisting of leaves and leaflets and by their light-

ened color and the characteristic purpling of the veins. The whole plant lags in growth, assumes a spindling habit, and produces very inferior fruit. An examination of the root-system of such a plant will reveal the fact that many of the roots and their branches, especially at their tips are decayed. The entire root-system, instead of presenting the ivory-whiteness of healthy tomato roots, has become discolored to a light buff or darker hue. In those roots most severely diseased the cortical tissue, if not already gone, may be easily slipped off between finger and thumb, leaving behind the more resistant vascular, woody tissue. If we compare the root-system of such a plant, artificially inoculated and grown in sterile soil, with that of a diseased plant grown in the field we shall find the two all but identical as to color, lesions, and manner of advance of the fungus within the roots.

FIELD STUDIES

Plate III, fig. 3, represents the appearance of a field in which many of the tomato plants had already succumbed to the blight. It will be seen from the figure that the disease does not uniformly affect all the plants in a row, but at first claims a host only here and there throughout the field, becoming more widespread and destructive as the season advances.

Failure to recover a causative organism from the aerial organs of diseased plants led us to make a more comprehensive study of their root systems. In order to determine whether or not a definite and consistent correlation obtained in the condition of the roots and the parts above ground it was necessary to remove the plants from the soil by hydraulic pressure. In this manner the entire plant could be washed out with but little injury to any part of the root system. And thus we were enabled to determine approximately the extent of damage suffered by different plants in varying stages of disease. This investigation of the roots was extended to include plants manifesting every degree of health, not excepting those showing no external symptoms of any diseases, whatever. Moreover, the work of washing out these plants was not confined to a single season, nor to one locality, but covered three seasons and included plants growing in such diverse soil conditions as obtain in the sandy loam of the Snake River bottom land, the basaltic soil near Pullman, Washington, and the porous, gravel drift of the Spokane Prairie. Upwards of two hundred individual plants were thus studied and careful notes made with reference to condition of parts above and below ground, with the result that, regardless of the character of the soil or variety of tomato, there was found to exist in every case a striking correlation between the diseased condition of the roots and the symptoms of disease shown in the foliage. To illustrate the degree of this correlation the following excerpt from notes made in 1910 is here inserted:

No of Plant	*Date*	*Condition of Foliage*	*Condition of Root System*
16	July 25	First symptoms very pronounced: leaves and leaflets show characteristic torsion; veinage purple; a few leaves becoming yellow.	Root system of 9 primary branches. Three of these diseased from a point where diameter is 1 mm. Many small roots near surface destroyed. Small laterals or "feeders" of the three diseased primary roots wholly destroyed.
12a	July 25	Yellow.	Nearly all small branches and feeders destroyed.
17	July 25	Badly blighted. In late stages: leaves all yellow or dying. Plant stunted.	All but one large root destroyed to within twelve inches of base of plant stem. Smaller branches all gone except those of the one remaining primary; and many of these are rotting.
10	Aug. 8	Diseased. In late stages: leaves yellow, twisted and brittle.	Of 20 primary roots, 11 are decayed from points varying from ½ inch to 12 inches from point of origin. Two of the remaining 9 primary roots were divided into 3 secondary branches. Showed no signs of decay as far out as uncovered (3 feet). Some small lateral branches of remaining seven primaries show decay.
12	Aug. 8	First unmistakable symptoms leaf torsion and general dulling of color of foliage. Habit, rigid.	Out of a total of 28 large roots, 6 were infected at from 12 to 36 inches of point of origin. Several rootlets destroyed.

The above tabulation of notes taken in the field at the time the plants were washed out will serve to illustrate the uniformity of relationship existing between the conditions obtaining in aerial and underground parts of individual plants.

Laboratory and Greenhouse Studies

Microscopic examination of living diseased roots revealed in every instance the hyphae of fungi confined at first to the cortical tissue, but subsequently extending to the phloem and xylem of the vascular tract. The discovery of these organisms in the root afforded a basis for further field and laboratory study the results of which, while they in no sense represent the last word on the subject of the yellow blight, may at least, be regarded as pointing the way.

During the summer of 1910 plate cultures of a considerable number of plants in various stages of blight were made in accordance with the following technique: The roots after being thoroughly washed and freed from clinging soil were placed in a flask containing a 1-1000 solution of mercuric chloride. After standing five to ten minutes in this solution they were washed in three changes of autoclaved water. They were next removed from the flask by means of flamed forceps and reduced to a finely divided pulp by running them over a close-meshed, sterilized sieve used as a grater. This root pulp was then placed in a flask of autoclaved water and dilutions were made from the mixture. From these dilutions were made the plate cultures, in which the medium employed consisted of tomato root or stem and leaf decoction added as a nutrient base to shredded agar. Other media were tried, but none proved any more satisfactory than the one containing tomato decoction.

Every attempt at isolation of root infesting organisms resulted in the appearance of one, or sometimes two, species of Fusarium*. The apparently constant presence of one or both of these species suggested to the writer their possible casual relation to the yellow blight. Hence, the next step was to determine whether by artificial means the disease could be produced by these two species of Fusarium, all other organisms being eliminated from the cultures.

Inoculation Experiments

In July, 1911, a series of experiments was started with a view to developing the blight artificially. Seed of the two varieties known as Sparks' Earliana and Truckers' Favorite was first subjected to fungicidal treatment by immersion for ten minutes in a 1-1000 solution of $HgCl_2$. The seed was next planted in common garden soil which had been sterilized in the autoclave at 120 degrees C. The seedlings, from their appearance above ground until the date of transplanting (August 17th to 30th) were irrigated only with sterilized water. Every possible precaution was observed in an effort to prevent accidental introduction of blight-producing organisms. Two hundred and sixty-five 6-inch flower pots were next filled with thoroughly pulverized garden

*Subsequently identified by Dr. H. W. Wollenweber, U. S. Dept. of Agr., as belonging to the section Elegans of the Genus Fusarium. The more constant species is *F. orthoceras*, App. & Wr., the less constant species is *F. oxysporum* (Schlecht).

soil and the whole lot thoroughly sterilized at 120 degrees C. One hundred and seventy-five of these pots were planted to Earliana seedlings, 80 of them being set aside as check plants. The remaining 95 were inoculated by placing a small fragment of spore-bearing mycelium of the suspected Fusarium species on the exposed roots of the intended host. In the same manner 46 Truckers' Favorite plants were inoculated from pure cultures of the same organism and 44 seedlings of this variety were set aside as check plants. Upon the recovery of these plants from the shock induced by transplanting they were all transferred at one time to the department greenhouse where they were kept throughout the fall and winter months of 1911. At this time we were unaware of the fact that the organisms associated with the disease in question are characterized by high optimum temperatures. The temperature of the greenhouse in which these plants were kept was at no time during the experiment equal to the optimum of *Fusarium orthoceras* or *F. oxysporum*. And this probably accounts in part for our failure to secure a quite typical symptomatic complex.

Owing to a protracted period of cold weather and failure to supply the greenhouse with sufficient heat fully six per cent of the inoculated plants were lost by freezing. Of those which survived, 38 manifested more or less typical symptoms of the characteristic blight, but in no case was the evidence above ground absolutely convincing. It was only after washing the roots of these plants free from soil and comparing them with the roots of the check plants that the diseased condition of the former was made more evident. From the roots of the blighted plants we were able each time to recover the organism used in inoculation as was later determined by comparison with the original cultures. Six additional plants showed only a trace of the disease in the roots.

Of the 90 check plants all but four were free from disease. From the surface roots of these four a species of Fusarium belonging to *Section Elegans* was recovered which, if not identical with, is closely related to *Fusarium oxysporum*.

PURE CULTURE INOCULATIONS

In order to determine the method of infection produced by the causative organism, seeds were removed from the interior of thoroughly ripe tomatoes and placed in tubes of slanted soil agar where, after five days they germinated. Transfer was then made from a pure culture of *Fusarium orthoceras* to each of several uncontaminated seedling cultures and placed in a culture chamber the temperature of which was approximately 21° C. (68.3° F.) Within 36 hours a visible growth of mycelium had developed. The hyphae soon spread in the direction of the young root and within 48 hours noticeable discoloration was apparent.

Four days after the inoculation of the seedlings several thin hand sections of a diseased radicle were made. These were mounted in water and examined with the microscope. Without the use of stains or other reagents the method of infection and progress of the invading hyphae were easily and distinctly visible.

Fig. 7, Plate IV, represents a section of the peripheral cells of an infected radicle and illustrates the habit of the organism and its manner of cell invasion. The infecting hyphae as shown in Fig. 8, Plate IV, grow from an already occupied cell directly through the cell wall into the neighboring cells. And as was frequently observed the cytoplasm in contact with the cell wall of a newly invaded cell is pushed in toward the center of the cell as much as 1½ mmm. by the hyphae which have effected an entrance through the cell wall. All infected cells speedily break down, their walls becoming yellowish and in time quite collapsed. Growth of the fungus within its host is both intercellular and intracellular. With the progress of the hyphae the cells rapidly come to be completely occupied with mycelium, the cortical tissue being the first to suffer. But in time the vascular tract is encroached upon and ultimately yields to the advancing parasite.

Cross-sections of the hypocotyl of the infected seedling showed no evidence of the fungus so long as any part of the root remained intact. With the destruction of the root there was always a gradual cessation of growth of the aerial portion of the seedling followed by loss of color and final collapse.

Repeated experiments involving the inoculation of tomato seedlings in pure culture invariably resulted in destructive infection, and this without previous mechanical or other injury having been suffered by the plants. The writer has demonstrated by these experiments and those involving artificial infection of potted plants the fact that in *Fusarium orthoceras* we have to do with a facultative saprophyte which in its relation to the tomato plant is a fungus of well-defined and vigorous parasitic character. Field and laboratory studies all go to show that invasion of the roots of the tomato does not necessarily depend upon infliction of mechanical injury upon these organs, though there can be no doubt as to such injury acting as a contributing factor in fields devoted to transplanted plants, subsequently carelessly cultivated.

As stated in another part of this paper, there seems good reason to believe that at least two varieties of *Fusarium oxysporum* are frequently found associated with *F. orthoceras* in the diseased roots of blighting tomato plants and have been isolated from the vascular tissue of the roots of plants killed by the disease. In the course of the studies upon this type of tomato blight the writer has prepared hundreds of permanent stained slides of transverse and longitudinal sections made from the roots of plants in every stage of the disease; but it should be

noted that with few exceptions these slides show hyphae only in the cortical tissue.

In August, 1913, Wollenweber reported having found Rhizoctonia in the roots of blighting plants collected at Hermiston and Hood River, Oregon. This discovery inclined Dr. Wollenweber to the opinion that Rhizoctonia may be an important factor in the development of the yellow blight. Culture experiments to determine the possible relation of Rhizoctonia to the yellow blight have not yet been made except in a preliminary way. Six healthy tomato plants transplanted to six-inch pots of unsterilized greenhouse soil were inoculated with *Fusarium orthoceras* and Rhizoctonia. A similar number of plants were inoculated with *Fusarium orthoceras* only, and a like number were planted without inoculation. These plants were kept for four months in the Arlington, Va., greenhouse at a temperature somewhat under the optimum for these two fungi. When the plants began to set fruit symptoms of blight became noticeable, but no differences could be noted between those inoculated with Fusarium alone and those inoculated with Fusarium and Rhizoctonia. In an effort to recover the two organisms from the several diseased plants positive results followed with reference to Fusarium, but Rhizoctonia appeared in none of the cultures. It is, therefore, barely possible that the inoculations with the latter parasite failed to result in infection. It should also be noted here that in none of the many plate cultures made during 1910 and 1911 were any colonies of Rhizoctonia observed, notwithstanding the fact that these cultures were made from plants representing the several stages of the disease from its incipiency to the actual death of the parts above ground. Just what part, if any, of this type of root disease is played by Rhizoctonia remains yet to be insevtigated. The optimum temperature for Rhizoctonia is essentially the same as that for the two species of Fusarium isolated from diseased plants. It would, therefore, seem reasonable that if Rhizoctonia is a prime factor in inducing this type of tomato blight the disease should have been reported from other parts of the United States, for Rhizoctonia may be found in cultivated soil almost anywhere in the United States, and is known to induce disease in the roots of many of our cultivated plants* including the potato. In their reference to the several plants subject to Rhizoctonia infection Stevens and Hall do not report the tomato as a host of this organism, nor does it appear until August, 1913, that Rhizoctonia has been observed as seriously affecting the tomato.

CULTURE STUDIES OF THE FUSARIUM SPECIES

Various media, including 1½ and 3% potato agar, potato cylinders, carrot agar, wheat heads, pear agar, tomato agar, stems of various plants including tomato, cotton and flax, and grains of corn and rice

*Stevens & Hall: Diseases of Economic Plants. P. 61, 1910.

were employed in the culture studies of the Fusarium species isolated from the diseased roots of plants grown in the field and those artificially inoculated and grown in the greenhouse. In addition to the foregoing, sterilized garden soil consisting chiefly of decomposed basalt was successfully used.

Of all media employed, steamed potato cylinders, boiled rice, and wheat heads produced the most abundant growth of aerial mycelium; whereas the soil cultures showed scant growth on the surface and a profuse subterranean growth. When grown on rice the sclerotia of *F. oxysporum* vary in color from light pink to a deep wine red. On steamed potato cylinders they are blue. This development of color is apparently influenced by temperature, for it was found on experiment that when cultures were incubated at 30° C. the hues were faint or in some cultures of *F. orthoceras* failed altogether. On the other hand, when subjected to a temperature of 18° C. or lower the colors were intensified, though less brilliant in *F. orthoceras*. These observations as to the possible influence of temperature on the depth of color agree with those recorded by Lewis, 1913*, in his studies of several disease-producing species of Fusarium.

Numerous efforts to produce the normal stages of the two species of Fusarium on the various kinds of agar media failed in whole or in part. But pure cultures grown on the young stems of woody plants or the older stem tissue of herbaceous plants such as the tomato or potato, or on heads of wheat resulted in the normal development of microconidia, macroconidia, and chlamydospores, provided the cultures were grown under conditions of favorable temperature and humidity. Of the various kinds of agar, best results obtained through the use of a 1½% potato agar. Wollenweber, 1913*, in his studies of the genus Fusarium, has found that when certain species are grown on boiled rice, potato or other starchy media certain secondary characters develop, characters which may not appear at all when the same species are grown on the steamed stems of woody or herbaceous plants.

Granting the importance of employing non-starchy media as a convenient method of securing the development of normal stages, in the life history of *Fusarium oxysporum* and *F. orthoceras* the writer has demonstrated by experiment that any radical change of one or more growth conditions may, regardless of the nature of the sub-stratum, induce abnormalities in the mycelium or in the number and kind of spores. These abnormalities, however, disappear when transfers are again made to non-starchy media and incubated at the optimum temperature and normal humidity, thus proving their physiologic nature.

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*Lewis, Chas. E. Comparative Studies of Certain Disease Producing Species of Fusarium. Bull. 219, Maine Agr. Exp. Sta., 1913.

*Wollenweber, H. W. Studies on the Fusarium Problem. Phytopathology: 3, 25: 1913.

To determine the possible effect of growth on the same kind of medium for a period of years, an isolation of *Fusarium orthoceras* made from the root of a diseased tomato plant on July 3, 1911, was transferred on July 31, 1911, to tomato agar consisting of a nutrient base of tomato root and stem decoction to which was added 12 grams of commercial agar to every liter of decoction.

From this culture, known as a1, transfers were made on Nov. 1, 1911, to tubes containing tomato agar of the same strength. On August 28, 1912, transfers from the November, 1911, cultures were made to tomato agar and allowed to dry out in the laboratory until September 24th, when they were used in making transfers to 1½% potato agar. In every instance the cultures were subjected to temperatures varying from 16° to 30° C. and throughout the growth of the fungus on tomato agar, a period covering 38 months, no noticeable variation affecting the cultural characters was observed. When transferred to lactose agar or 1½% potato agar the growth of mycelium was vigorous and noticeably more abundant than when grown on tomato agar. *F. orthoceras*, grown on lactose agar, produces marked sub-aerial growth, whereas when grown on tomato or potato agar, the growth is almost wholly aerial.

THE TEMPERATURE FACTOR

Field observations covering several seasons invited the inference that the influence of temperature as a factor in the development of the root-infesting organisms might be of considerable importance. To secure data on this and other questions such as previous treatment of land now devoted to tomatoes, methods of transplanting, cultivation, etc., the writer secured the co-operation of 62 tomato growers, most of whom live in the Yakima and Snake River Valleys. It was reported by all but six or eight that in their opinion the heat and wind greatly accelerated the disease. These deductions were not founded upon ascertained facts regarding soil temperature, light intensity, wind movement, etc., but upon investigation it has been found that a certain and definite relation exists between the temperature of the medium in which the roots grow and the appearance and severity of the disease. Many growers have for years made it a practice to transplant their tomato plants in from six to eight inches of soil and usually very much to their profit owing to the consequent reduction in the number of blighted plants.

On the 14th of May, 1911, 467 healthy, vigorous plants were planted in an open, unshaded field previously devoted to wheat. These plants were set in holes varying in depth from four to six inches. They were frequently irrigated and received sufficient cultivation to give them every possible advantage through maintenance of favorable tillage. The following tables give the results of field observations made on two separate occasions during the season of 1911:

TABLE I.

Variety	Field Age	No. of Plants	Date of Observation	Atmospheric temperature at Lewiston, Idaho, for ten days prior to July 11, 1911. Maximum	Minimum	Mean	Blighted Plants No.	Per cent.
	Days			July 1, 79°F	54°F	66°F		
Sparks' Earliana	58	32	July 11, 1911	July 2, 85°F	56°F	70°F	24	75.0
Chalk's Early Jewel	58	150	July 11, 1911	July 3, 81°F	63°F	72°F	94	62.6
Livingston's Beauty	58	74	July 11, 1911	July 4, 85°F	61°F	73°F	42	56.7
Ponderosa	58	77	July 11 1911	July 5, 94°F	56°F	75°F	57	74.0
Dwarf Champion	58	85	July 11, 1911	July 6, 89°F	64°F	76°F	24	28.2
Truckers' Favorite	58	49	July 11, 1911	July 7, 72°F	58°F	65°F	19	38.7
				July 8, 77°F	55°F	66°F		
				July 9, 80°F	51°F	66°F		
				July 10, 82°F	5°1F	66°F		

TABLE II.

Variety	Field Age	No. of Plants	Date of Observation	Atmospheric temperature at Lewiston, Idaho, for seven days prior to observation. Maximum	Minimum	Mean	Blighted Plants No.	Per cent.
	Days							
Sparks' Earliana	65	32	July 18, 1914	July 11, 90°F	50°F	70°F	26	83
Chalk's Early Jewel	65	150	July 18, 1914	July 12, 94°F	53°F	74°F	110	73
Livingston's Beauty	65	74	July 18, 1914	July 13, 100°F	59°F	80°F	52	70
Ponderosa	65	77	July 18, 1914	July 14, 96°F	70°F	83°F	61	79.2
Dwarf Champion	65	85	July 18, 1914	July 15, 104°F	63°F	84°F	39	45.8
Truckers' Favorite	65	49	July 18, 1914	July 16, 106°F	67°F	86°F	30	61.2
				July 17, 100°F	68°F	84°F		

The temperatures recorded in the foregoing tables were obtained through the courtesy of the Weather Bureau, Department of Agriculture. While they probably do not represent actual temperature conditions for the tomato field in which the experiment was conducted they at any rate approximate closely the prevailing temperatures throughout that part of the Snake River Valley. Unfortunately soil temperature curves were not obtained in the field; but the writer's studies of the records of atmospheric and soil temperatures (the latter taken at two and four inches depth) for Pullman and vicinity and for Arlington, Va., have been sufficiently extensive to justify the conclusion that the soil temperature at four inches depth in an open tomato field would be roughly that of a curve representing the mean atmospheric temperature. At two inches depth, experience has shown that the mean soil temperature for a given period is during the months of June, July, and August actually higher than that of the immediate atmosphere.

Experiments conducted in the laboratory where temperature conditions were controlled demonstrated the fact that maximum, minimum, and optimum temperatures for the two species of Fusarium were approximately the same for each, namely, 37°, 4°, and 30° C. or 95.9°, 39.2°, and 86° F. Although the optimum temperature is relatively high, both laboratory and field studies indicate the fact that both *Fusarium orthoceras* and *F. oxysporum* have marked infective power at temperatures as low as 65° F. The rate of growth of the mycelium at 65° F. shows a marked decrease as compared with that of cultures of the same strain when maintained at 86° F. For example, visible growth may be seen within 20 hours at optimum temperature; whereas at 65° F., the same extent of growth is attainable in hardly less than 36 hours. This latter fact when contrasted with the recorded observation that, for the region in question, the month of July marks the period of maximum evaporation and low relative humidity, may throw some light upon our attempt to account for the excessive amount of blight during that month.

Owing to lack of facilities for experiments in which the several factors could be controlled and their effects measured, it is obviously difficult to determine to what extent the relative humidity, rate of wind movement, and intensity of light and heat are factors in an epidemic of blight. It hardly need be pointed out, however, that the sum of the influences of these several factors, expressed in terms of evaporation from exposed leaf surface, must exert a very decided effect upon plants whose roots are reduced in functioning power. Given any tomato plant in the incipient stages of the disease with the minute, ultimate branches of its roots already destroyed, it but needs a soil temperature of 80° to 90° F. to bring about the destructive invasion of the complete root system. Naturally, in the field, high soil temperature follows closely upon increased atmospheric temperature. If on the hottest days, there

is also considerable wind movement, the rate of evaporation will be accelerated, and the vitality of the plant diminished. This diminished vitality is expressed in a general cessation of growth in every part of the plant and a systemic impairment of functioning power. It needs yet to be determined what physiologic processes underlie the characteristic torsion and color change of the leaves and the fact that wilting, if it occurs at all, does so only at the very last.

Field observations made in 1910, 1911, and 1912 by the writer unmistakably indicate the potency of light intensity as a factor in accelerating the yellow blight. For example, it is a well-known fact that where a slight degree of shade is afforded by orchard or other trees there are relatively fewer diseased plants than where tomato plants of the same variety are grown in similar soil, but in open situations exposed to the maximum of direct sunlight. It might be argued that this difference in percentage of blighted plants could be due to difference in soil temperature; but in either case the ground is shaded by the dense growth of tomato plants to such extent that the soil temperature factor would not be appreciably affected.

Livingston, 1911*, has shown that the rate of water loss from living foliage as well as from exposed soil is considerably greater than that recorded by the white porous clay atmometer cups devised and used by him in his evaporation studies. This increased water loss is due to the fact that when plants are exposed to direct sunlight their foliage absorbs more of radiant energy than obtains in the case of shaded or semi-shaded plants. This absorbed energy causes a rise in temperature of the contained water and a consequent conversion of water to water vapor. Thus it is that in the case of diseased plants suffering from invasion of their roots by destructive fungi any factor tending toward increased water loss from the leaves becomes an inhibitive factor and hastens the physical decline of the host.

DESCRIPTION OF THE TWO SPECIES OF FUSARIUM

According to Wollenweber's† classification, 1913, both *Fusarium oxysporum* and *F. orthoceras* belong to the *section Elegans*. Other species belonging to this section are *F. lycopersici* Sacc., a vascular parasite of the tomato causing a well-known wilt disease in this Country and Southern Europe; *F. niveum* Smith; *F. vasinfectum* Atk., a vascular parasite infecting the roots of the cotton plant; *F. tracheiphilum* Smith; *F. redolans* Wollw., and *F. conglutinans* n. sp.

Fusarium orthoceras differs from *F. oxysporum* in the absence of pinnotes, sporodochia, and sclerotia. Also it differs in the fact that triseptate conidia number about 15% of the total number of conidia produced in a normal culture; while in *F. oxysporum* triseptate conidia

*A Radio-atmometer for comparing Light Intensities. Plant World 14, pp. 96-99.
†Loc. cit., p. 28.

are prodigiously numerous and 4- and 5-septate conidia constitute up to 25% and 10% respectively the spore output of a normal culture.

Cultures of these two species of Fusarium on sterile basaltic soil invariably produce an abundance of chlamydospores, their development apparently increasing upon loss of moisture from the medium. This being true, it naturally follows that in those sections where the yellow blight is most serious, the soil moisture and temperature conditions which obtain during August and early September are almost ideal for the production of chlamydospores. The continued planting of tomatoes in the affected sections of the State must in time result in serious soil infection to the end that, unless present methods of tomato culture are improved it must result in continued and increasing crop devastation.

In October, 1912, some root remains of tomato plants killed by the yellow blight were collected from a Clarkston (Wash.) field and examined under the microscope for the presence of hyphae. Small bluish areas were observed to occur throughout the vascular tissue of these dead roots which, in section, when microscopically examined proved to be sclerotial tissue of some fungus. Subsequently these roots were cut into thin bits or shavings and placed in small paste-board boxes, where they remained five months subject to the out-door winter conditions which obtained in Southeastern Washington during the season of 1912-1913. Following this period the root-sections were kept dry in the laboratory eleven months. They were then washed ten minutes in a 1-1000 solution of mercuric chloride, rinsed in several washings of sterile water and incubated in test tubes at the optimum temperature of *Fusarium orthoceras*. Within forty-eight hours a small percentage of these chips had become white with mycelium of a species of Fusarium which upon further study proved to be a variety of *F. oxysporum*. Doubtless these masses of viable hyphae, hundreds of which may develop within one of several main root branches of a diseased plant, are important factors in the propagation of the parasite.

The two species of Fusarium identified with yellow blight are exceedingly prolific in the production of thick-walled, warty chlamydospores in addition to the micro- and macroconidia. The length of time these chlamydospores may remain viable has not been ascertained, but it is certain that cultures may be obtained from them at the close of a two-year period of desiccation in test tubes kept under ordinary laboratory conditions.

CONTROL STUDIES

Owing to the fact that we are here concerned with a disease probably induced primarily by one or more root-destroying fungi the effects of which are augmented by varietal susceptibility and by such external factors as rapid loss of water from the leaves, excessive intensity of sunlight, and abundance of soil moisture, the problem of control offers difficulties which have not yet been overcome. Moreover, the ques-

tion of control of this type of tomato blight is further complicated by the fact that the active organisms are not obligate parasites, but are facultative saprophytes capable of remaining virile through several seasons. Experience covering a period of many years has shown that the causative organisms are present in the soil regardless of the nature of its treatment or the kind of crop or crops grown in any given field prior to its being planted to tomatoes.

During the summer of 1911 the Washington Experiment Station conducted an experiment at Clarkston, Washington, involving the planting of 1262 plants as follows: (1) 500 plants of six varieties on soil which had been for many years devoted to the growing of wheat; (2) 300 plants of four different varieties planted in an old peach orchard in which tomatoes had not previously been grown; (3) 62 plants of one variety grown in a garden where tomatoes had been grown in former years; (4) 400 plants in virgin sage-brush soil. The object of this experiment was to secure data on the relation of blight prevalence to previous cropping and treatment of soil. The results were as follows: Field No. 1, plants of 65 days field age showed 63.5% of blight; Field No. 2, plants of the same field age and the same varieties showed 34.6% of blight. Field No. 3 was planted to Sparks' Earliana plants and may be disregarded so far as it concerns this experiment, though it is of interest to note that of the 62 plants in this lot all but seven succumbed to the blight. Observations recorded during the same season relative to the occurrence of blight in fields previously devoted to tomatoes go to show that the disease affected as few as 3% of the plants in some fields and as high as 90% in others. In Field No. 4 the majority of the plants were destroyed, probably by cut worms, but of the surviving few, not a single plant manifested any symptoms of blight. To ascertain whether or not the popular belief in the absence of the tomato blight organisms from the virgin soil of the Clarkston country is well founded it will be necessary to conduct experiments covering a period of at least six years. One grower reported in 1912 the occurrence of blighted plants among those he had planted in "new" soil; and it is not unlikely that further study will show like results.

The above experiments supplemented by data obtained from 62 growers would seem to indicate the futility of crop rotation as a possible means of control. At least, it may be said that no system of crop rotation has been discovered the practice of which will materially affect the occurrence of tomato blight.

From our own observations and from occasional reports from growers, it seemed likely that the occurrence of the yellow blight might in some measure be traced to the practice of transplanting from the hot-bed directly to the field, or from hot-bed to cold-frame and then to the field. In order to obtain data on this phase of our study of the disease a questionnaire was prepared and sent out to as many

tomato growers as had expressed a willingness to co-operate with us. It was also conceived that by giving individual plants an opportunity to grow to maturity without subjecting them to the severe shock incident upon transplanting susceptibility to invasion by the causative organisms might be materially diminished. Moreover, an effort was made to place each individual under hot-house conditions in order to force its development and give it every possible advantage during the first few weeks of its growth. In order to accomplish this result, three or four sound seeds were planted in a place at intervals of three to four feet apart in the row. Over each planting was placed a glass-covered box* measuring 12 in. x 12 in. x 12 in. The glass cover was held in place by opposite grooves and could be removed as soon as the plants had attained sufficient size to require no further forcing. By planting four seeds to a hill we had opportunity to select the most robust and promising by removing the other three.

In 1912, two hundred of these forcing-boxes were installed, half of them in a tomato field in Clarkston and the remainder on the College farm in a field where, during the summer of 1911, the writer recorded from 32-34% of loss from yellow blight. The Clarkston experiment, owing to lack of proper care, did not constitute a satisfactory test; though it should be said that of the one hundred plants, but three of them showed any symptoms of blight, and this at a time when the disease had reached its maximum severity. Check-rows of transplanted plants alongside those grown under the forcing-boxes blighted much more freely, but were so over-run with weeds as to make the experiment almost valueless. Throughout the neighborhood, however, transplanted plants were blighting in percentages ranging from 4% to 93%.

The one hundred test plants grown on the College farm at Pullman were in a field which was thoroughly cultivated and kept free from weeds, thus affording every advantage to the plants throughout the experiment. The glass cover was not removed until the plants had attained a height of at least six inches, after which time they were allowed to grow up and over the boxes which served to support them and thus keep the fruit from contact with the soil.

At the close of the season, late in September, the percentage of blighted plants throughout the field and on either side of the experimental row amounted to 1.5%, though in some parts of the field the diseased plants numbered as many as 4%. All plants not grown within the forcing-boxes had been transplanted from hot-beds directly to the field. The experimental row was planted in the midst of the field and directly through that part of it where, in the summer of 1912, the percentage of diseased plants reached a maximum of 45%. Not

*The cost of these boxes, including glass cover, need not exceed 25 cents per box, and with proper care they may be used several seasons.

one of the plants grown from seed under the forcing-boxes showed any symptoms of blight. Moreover, they all made a more rapid and vigorous growth, than those not thus grown. To be sure, we can not present this as a satisfactory test of the merits or shortcomings of this method of growing tomatoes, but it is reasonable to hope that the use of the forcing-boxes points the way. The writer has never seen the yellow blight appear among plants left standing in hot-beds or cold-frames, though two Clarkston tomato growers report having observed a limited number of diseased hot-bed plants which had never been disturbed. It is not improbable that such instances of blight may be traceable to root injury.

It is a well-known fact that when tomato plants are finally transplanted in the field they suffer a shock so severe in some cases as to preclude any chance of recovery. Other plants may scarcely wilt, but all do, nevertheless, receive a genuine shock, the full recovery from which requires from five to eight or more days. Many of these plants in being transferred from the hot-bed or the cold-frame to the field may receive serious root injury, and thus be rendered the more susceptible to invasion by wound fungi or more virulent facultative saprophytes such, for example, as *Fusarium orthoceras* or *F. oxysporum*.

Carelessness in cultivation of the transplanted plants often results in injury to those roots which may have come to occupy the surface soil to a depth of three to five inches. It has been observed that growers are sometimes in the habit of running their cultivator teeth within three or four inches of the plants—a practice apt to inflict injury to the roots in soil, the July and August temperature of which favors a rapid and vigorous development of the attacking fungi.

Although the experiment was not tried, judging from such results as have already been obtained, it is not unlikely that in so far as it may be practicable, the exact duplication of hot-house conditions would prove productive of a minimum of blight. The manure used, a forkful or more to each hill, should be thoroughly composted. This will go far toward the reduction of heat so often observed in less thoroughly rotted manures. By this individual hot-house or forcing-box method one may safely plant tomato seed several weeks earlier than is customarily regarded as a safe date for transplanting from hot-bed or cold-frame. Moreover, the plants thus grown in the field suffer no shock and are afforded every advantage, to enable them to bear fruit earlier, a thing commercially desirable, inasmuch as it means early marketable fruit.

Essary*, 1912, has shown that through selection for "blight" resistance we have recourse to a method whereby the grower may practically eliminate that type of tomato blight described by him in Bull.

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*Essary, S. H. 1912. Notes on Tomato Diseases, with Results of Selection for Resistance. Tenn. Agr. Exp. Sta. Bull. 95.

95 of the Tenn. Agr. Exp. Sta. Our own studies have repeatedly shown that certain varieties of tomato, e. g., Livingston's Dwarf Champion, are less susceptible to yellow blight than others. By crossing and selection it is not unlikely that the excellent qualities and high productive power of Sparks' Earliana or Bolgiano's IXL might combine with the vigor and blight resistance of the Dwarf Champion to yield an excellent market tomato slightly or not at all susceptible to the yellow blight organisms.

Experiments involving use of chemicals were tried, the results of which go to show that any treatment severe enough to check the development of the parasite was also an effective deterrent to the growth and vigor of the host. These experiments were confined to the use of the following fungicides: Copper sulphate solution in the ratio of 1 lb. of the salt to 2.5 gallons of water; Pyxol, a standardized disinfectant; Crest Spray, a distillate made from the refuse of fir stumps; and Nicene, a fungicide prepared by the Hood Chemical Company of Chicago. The following tabulation of the technique and results has been furnished through the kindness of the assistant pathologist, D. C. George, to whom this part of the problem was assigned.

Test tubes containing 10 cc. of potato agar were treated as follows:

Nicene Treatment

Series A—5 tubes to each of which was added 0.01 g. of Nicene.
Series B—5 tubes to each of which was added 0.25 g. of Nicene.
Series C—5 tubes to each of which was added 0.50 g. of Nicene.
Inoculated with *Fusarium sp.* on Dec. 12, 1912.

Results

Series A—Growth of fungus in each tube of the series.
Series B—Growth of fungus in each of three tubes.
Series C—No growth.

Crest Spray (Undiluted)

Series A—5 tubes to each of which was added .05 cc. of the spray.
Series B—5 tubes to each of which was added .10 cc. of the spray.
Series C—5 tubes to each of which was added .25 cc. of the spray.
Result: No growth in any of the tubes.

In another trial the fungicide was diluted to 1/50 of its normal strength. Result: Excellent growth of fungus in all tubes in Series A and B, but none in Series C.

Pyxol (A Standardized Disinfectant)

Series A—5 tubes to each of which was added .05 cc. of a 1-56 solution.

Series B—5 tubes to each of which was added .10 cc. of a 1-168 solution.
Series C—5 tubes to each of which was added .15 cc. of a 1-224 solution.
Result: Growth in all but two tubes of Series C.

COPPER SULPHATE (1 LB. TO 2.5 GALLONS OF WATER)

Series A—5 tubes to each of which was added .05 cc. of solution.
Series B—5 tubes to each of which was added .10 cc. of solution.
Series C—5 tubes to each of which was added .25 cc. of solution.

RESULTS

Series A—Growth of Fusarium in three tubes.
Series B—Growth of Fusarium in three tubes.
Series C—No growth.

SUMMARY

1. The type of tomato blight considered in this bulletin is apparently typical of the Upper Sonoran Zone of the Pacific Northwest.

2. It is primarily a root disease due wholly or in part to two species of Fusarium.

3. From roots of plants in various stages of blight were isolated *Fusarium orthoceras* App. a. Wollw. and at least two varieties of *Fusarium oxysporum* (Schlecht).

4. Controlled inoculation experiments resulted in the artificial production of blight in nearly all inoculated plants. From the roots of these plants the specific organisms were recovered.

5. The causative organisms are characterized by a relatively high optimum temperature. When the soil temperature rises to near the optimum the first symptoms of blight appear. With rise of soil temperature the virulence of the parasites increases and the blight becomes general.

6. Inoculation of tomato seedlings in pure culture resulted in prompt and severe infection of root system, the aerial portion of the plants remaining free from hyphae until the roots were destroyed.

7. Exposure to intense sunlight and wind tends to influence rate of evaporation and thus renders the plants more susceptible to the disease.

8. *Fusarium orthoceras* and *F. oxysporum* produce an abundance of chlamydospores in the soil. It is also possible that these species are readily propagated by perrenating mycelium formed in the roots of blighted plants.

9. Owing to the fact that the causative organisms are present in the soil and infect underground structures any practical method of soil treatment by fungicides has not been worked out.

10. Crop rotation or planting on virgin soil are of doubtful preventive value.

11. Greatest freedom from the disease obtains wherever the practice of transplanting from hot-bed to cold-frame or directly in the field has been abandoned.

The author wishes to express his appreciation of valued assistance rendered by N. Rex Hunt, now of the United States Department of Agriculture, and the several tomato growers of the Pacific Northwest, whose co-operation made possible a knowledge of many salient facts. Of special importance to the completion of this bulletin was the assistance given by Mr. D. C. George, Assistant Plant Pathologist of the Washington State Experiment Station.

EXPLANATION OF PLATES

All drawings were made with aid of camera lucida except Fig. 6, Plate IV, which was made with the Edinger drawing apparatus.

The Zeiss 2 mm. N. A. 1.30 homogeneous oil immersion and No. 4 ocular or their equivalents were used in all cases except Figures 1-4, Plate V, for which a Zeiss 4 mm. objective and No. 4 ocular were used.

PLATE I—

Diseased and healthy plants of same age.

PLATE II—

Fig. 1. Root-systems of two tomato plants of same age grown under like conditions of climate, soil, irrigation, and cultivation. The one on the left is that of a plant in normal health, the other is that of a plant in last stages of the blight.

Fig. 2. Root-systems of two plants in two different stages of disease.

PLATE III—

Figs. 1 & 2. Plate cultures of *Fusarium spp.* obtained from diseased roots of blighting tomato plants.

Fig. 2. Field near Clarkston, Wash., in which more than 60% of the plants succumbed to yellow blight.

PLATE IV—

Fig. 1. Hyphal branch of *Fusarium orthoceras* bearing conidia.

Fig. 2. Conidia of *F. orthoceras* produced in pure culture on sterilized garden soil.

Fig. 3. Macroconidia of *F. orthoceras* grown in pure culture on sterilized tomato stem.

Fig. 4. Immature chlamydospore of *Fusarium orthoceras* grown in pure culture on tomato agar. An aberrent type of chlamydospore from same culture.

Fig. 5. Terminal, lateral, and intercalary chlamydospores of *Fusarium sp.* grown in pure culture on sterilized garden soil.

Fig. 6. Part of cross section of root of tomato seedling grown in pure culture inoculated with *F. orthoceras.* Note progress and character of infection from periphery toward interior of root.

Fig. 7. Part of cross section of a seedling root showing invasion of another host cell.

Fig. 8. Cross section of infected root of blighted plant showing mycelium in cortex, phloem, and xylem.

Fig. 9. Longisection showing hyphae within cells of cortex.

Fig. 10. Longisection showing hyphae within cells of phloem.

Fig. 11. Longisection of vascular tissue of plant killed by root-infesting Fusaria.

Fig. 12. Haustoria (?) formed at ends of short hyphal branches of *Fusarium sp.*

PLATE V—

Fig. 1. Fragment of mycelium and spores of Fusarium from culture isolated from root of blighted tomato plant obtained after 12 months of desiccation in laboratory.

Fig. 2. Conidia of *Fusarium orthoceras* grown at temperature of 30° C.

Fig. 3. Fragment of mycelium and spores of *F. orthoceras* grown at temperature of 35° C.

Fig. 4. Microconidia of *F. orthoceras* grown at temperature of 35° C. Note reduced size of spores.

PLATE I.

Plate II.

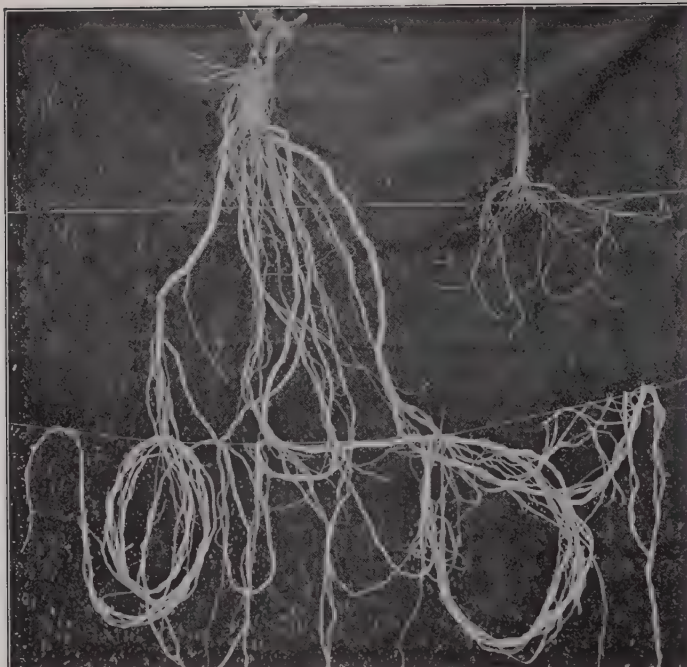


Fig. 1.

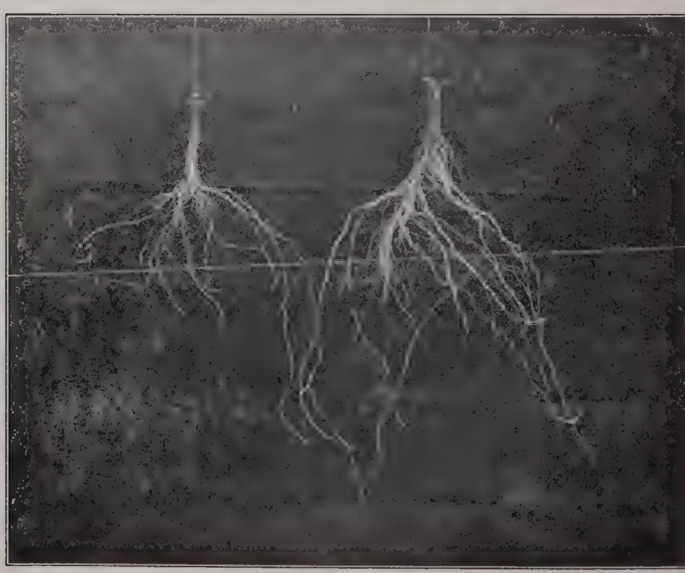


Fig. 2.

PLATE III.

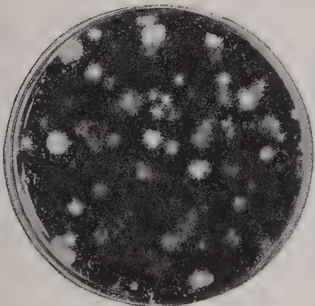


FIG. 1.

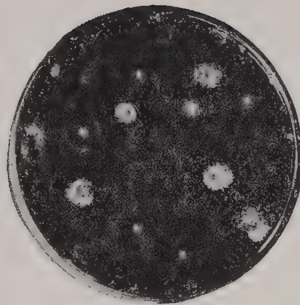
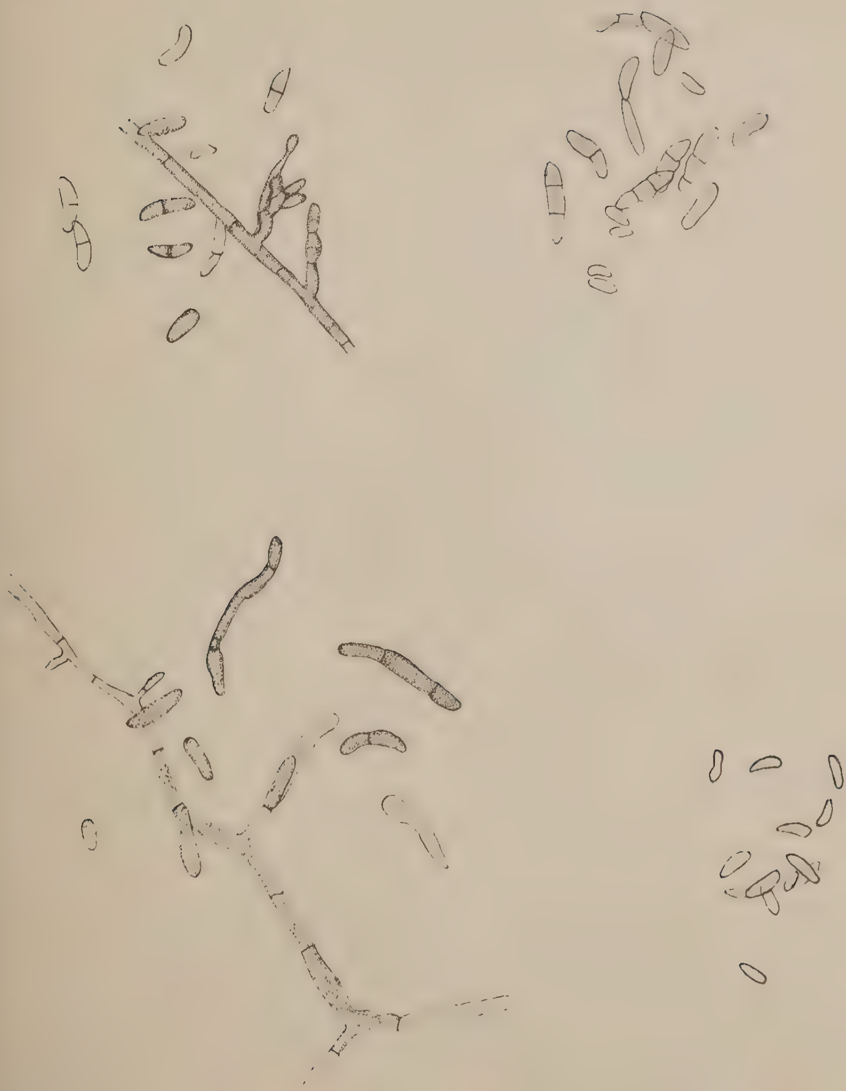


FIG. 2.

FIG. 3.

PLATE V.



H. B. H. Del.